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The problems involved in the characterisation of scolopendromorph species (Chilopoda: Scolopendromorpha)

by

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ABSTRACT

Difficulties encountered in achieving correct identifications of scolopendromorphs are detailed, and the need for work on variation is stressed. The causes of this variation are examined with particular reference to scolopendrids and *Cryptops*. Many of the characters used in specific determination cannot be explained in terms of their function, and it is suggested that many are the result of non-adaptive variation controlled by neutral alleles. Alternatively, some may be species recognition characters. It is also suggested that the number of described species is too high, although it may sometimes be difficult to decide whether one or several species are involved. The need for accurate illustrations and a standard terminology are stressed.

INTRODUCTION

Many of the difficulties encountered when attempting correct identifications of scolopendromorphs are of our own making. Problems arise from poor observation, inadequate description, lack of knowledge of the literature and descriptions based on juvenile specimens. In addition, the allocation of some common species to the wrong genus has resulted in the naming of spurious new species. There are also problems of comprehension arising from translation from one language to another and inaccurate or misleading terminology. Descriptions all too frequently lack accurate illustrations. Crabill (1960) noted the 'ruck' of German terms -*Sporne, Höcker, Spinen, Zapfen, Borsten, Sägezähne* and *Dornen* for the setae, spines, spurs and other armature in the great monographs. He pointed out that to ensure our understanding of one another it was desirable to establish a uniform terminology. This is something that has yet to be achieved.

In addition to the above problems, the nature of the animals themselves make the Scolopendromorpha a very difficult group taxonomically. Shelley has written of the taxonomy of neotropical *Scolopendra* species (e-mail dated 28.01.02): that it 'is a monumental mess, the toughest myriapod problem I know of … and also one that, almost surely, will never be solved, for I cannot imagine anyone being willing to devote his/her life to straightening out something this mind-bogglingly complex, and there are so many available names that would have to be evaluated.' He also proposed that for *Cryptops* there should be a moratorium on new species proposals until the existing names can be re-evaluated using scanning electron microscopy (Shelley 2000).

Scolopendra, Otostigmus, Alipes, Ethmostigmus, Rhysida, Cryptops and *Scolopocryptops* need taxonomic attention; indeed it is probable that almost all scolopendromorph genera require complete revision.

THE IMPORTANCE OF WORK ON VARIATION

In addition to the re-examination of type material, further data are required on variation if meaningful decisions are to be made on the status of chilopod populations. This has been stressed by a number of workers. Thus Würmli (1974) concluded that the characters used in the Scutigeromorpha need to be reassessed and variation described in much greater detail. Tobias (1974) stated that it seemed necessary to make a complete reassessment of the existing classification of the Lithobiidae and that variation should be measured in populations from a complete range of a species. Her opinion was echoed by Eason who in a letter to the author dated 21.9.1995 wrote: 'Intraspecific variability in Lithobiomorpha is so vast that it is extremely difficult to define species accurately and quite impossible to construct foolproof keys for their identification. I am now faced with the problem of amalgamating five nominal species, which some authors believe to be distinct, into a single variable species, after examining 200 specimens.' Misioch (1984) believed that 'there is strong evidence that the comparatively high numbers of specific and subspecific names based on Central European forms (of Geophilomorpha) is caused much more by variation than by specific diversity.'

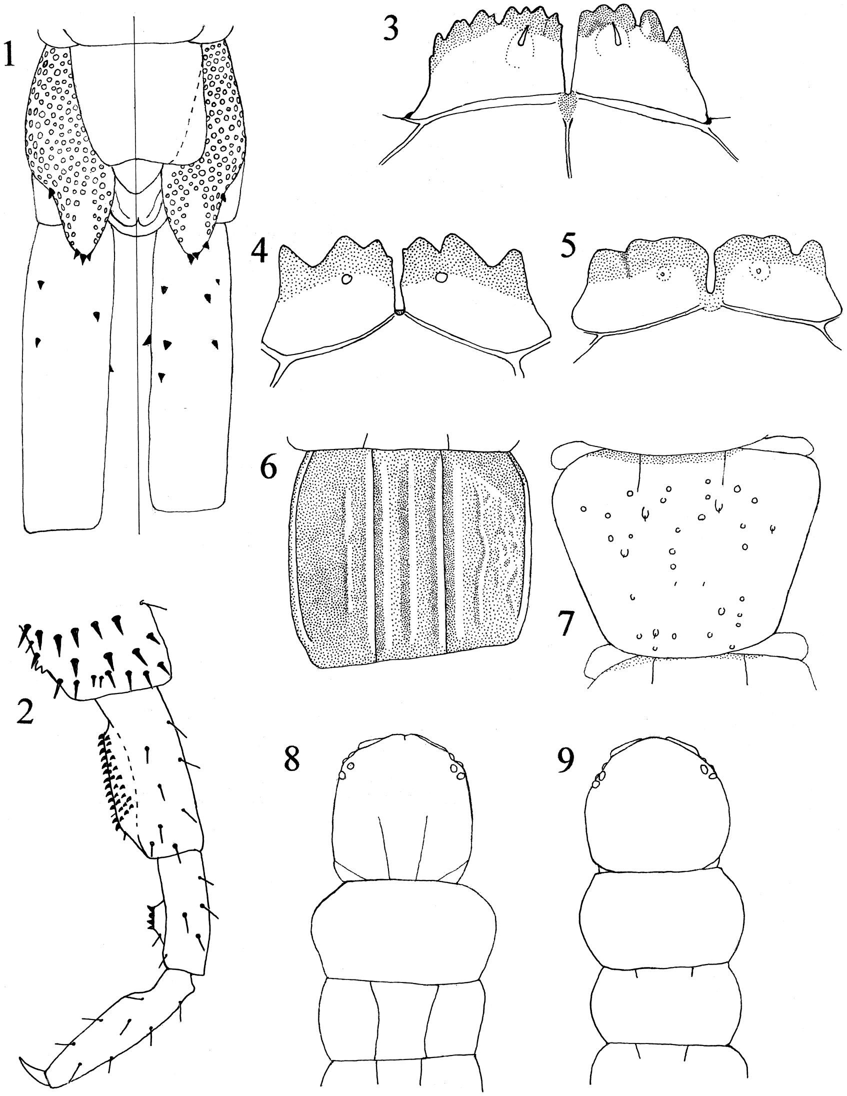
CAUSES OF VARIATION IN SCOLOPENDROMORPH CENTIPEDES

The problems posed by individual variation in scolopendromorphs have long been recognised. In 1892 Pocock wrote: 'The genus *Otostigma,* is exceedingly difficult to understand; and it is impossible to feel absolute confidence in the stability of a species, especially when it is based on a single example.' Attems (1934) regarded *Otostigmus* as the most difficult scolopendrid genus, pointing out that morphological characters were very variable, making specific discrimination a considerable problem. Kraepelin (1908) described variation in *Cryptops australis* Newport, 1844, and more recently, Lewis (1978) discussed variation in scolopendrid centipedes, while Lewis (1989) and Schileyko & Minelli (1998) have done the same for *Newportia.* An attempt is made here to list the types of variation in the light of recent information and with particular reference to Scolopendridae and *Cryptops*.

Sexual dimorphism

In male *Scolopendra morsitans* Linneaus, 1758, the prefemora, femora and tibiae of the end legs are flattened dorsally and have a marginal ridge. There are cylindrical processes on the prefemora of the end legs in males of some species of *Alipes, Digitipes* and *Otostigmus* (subgenus *Parotostigmus*). Other sexual modifications of leg 20 and tergite 21 in neotropical species of *Otostigmus* have been well documented (Lewis 1981). Attems (1934) suggested that in some *Otostigmus* species the shape of sternite 21, with sides parallel or diverging posteriorly as opposed to converging (Fig. 1), might be a male character. Lewis (1982) suggested that the presence of spines on the tergites might be a female secondary sexual character in *Otostigmus spinosus* Porat, 1876.

The twentieth pair of legs in male *Cryptops* often (always?) has numerous short setae ventrally, and in some New Zealand species this character is seen on more anterior legs. In addition, in the New Zealand species *Cryptops polyodontus* Attems, 1903 (Fig. 2) and *Cryptops lamprethus* Chamberlin, 1920, there are, very unusually, several rows of teeth on the tibia of the end leg and the teeth on the tarsus are borne on a keel (Archey 1924).



Figs 1–9. Characters of Scolopendromorpha. 1. Composite drawing showing a ventral view of segment 21 and end leg prefemora, based on *Rhysida* and *Otostigmus*. The left side with three coxopleural end spines and one lateral spine, regularly arranged prefemoral spines and sternite 21 narrowed posteriorly (also indicated by dashed line on right). The right side with two coxopleural end spines, two lateral spines, an irregular arrangement of prefemoral spines and sternite 21 widened posteriorly. 2. Distal part of femur, tibia and tarsi of an end leg of *Cryptops polyodontus* Attems, 1905 from Zealand (after Archey 1924). 3. Coxosternal toothplates of a male *Scolopendra morsitans* Linnaeus, 1758, length 78 mm, showing right tooth plate with additional teeth from Île aux Sables, Rodrigues, Indian Ocean. 4. Normal coxosternal tooth plates, of a 35 mm specimen of *Otostigmus beroni* Lewis, 2001 from Nepal. 5. Worn coxosternal tooth plates of a second 35 mm specimen of *Otostigmus beroni*. 6. Tergite 10 of a 30 mm *Otostigmus* nr *scaber* Porat, 1876, from Gunung Mulu, Sarawak. 7. Sternite 17 of a 45 mm specimen of *Otostigmus* cf *sumatranus* Haase, 1887 from Gunung Api, Sarawak. 8. Head and first two tergites, of a 38 mm specimen of *Cormocephalus cupipes* Pocock, 1891 from Mozambique (after Lewis 2001). 9. Head and first two tergites of a 38 mm specimen of *Cormocephalus pseudopunctatus* Kraepelin, 1903 from Mozambique (after Lewis 2001).

As scolopendromorphs are often difficult to sex without dissection, or in the case of small species, clearing, and the sex of specimens is rarely given, there is still a real possibility that conspecific males and females have been described as distinct species. Verhoeff (1931) showed that *Cryptops savignyi* (= *anomalans*) *hirtitarsis* Brolemann, 1928, which lacks dense fine setae on tibiae and tarsi I and II of the end legs is the male of the species.

Changes during post larval development

Lewis (1968) described morphological changes during development in a Nigerian population of *Scolopendra amazonica* Bücherl, 1946 (= *S. morsitans* and referred to as *S. morsitans* below) and in three species of *Otostigmus* (Lewis 2000). Antennomere number increased with age but whereas the number of glabrous antennomeres and the number of tergites with paramedian sutures and margination increased in *S. morsitans*, they did not change in the *Otostigmus* species. Older individuals sometimes develop additional coxosternal teeth, which can mask the typical pattern (Fig. 3), so that young animals may offer the clearest characters in this respect. When dealing with single specimens it is sometimes impossible to decide whether the tooth pattern represents the norm or not.

Kraepelin (1908) noted that in *C. australis*, the shape of the anterior border of the coxosternum and the number of setae thereon changed with age, as did the number of teeth on the tibiae and tarsi I of the end legs, the number of coxal pores, and the extent of the pore fields. This was not always appreciated by subsequent workers, with the result that different stadia have been described as different species, for example *Cryptops navis* Chamberlin, 1930 and *Cryptops sinesicus* Chamberlin, 1940 (Lewis, unpublished data). The extent of tergal paramedian sutures also changes with age in some *Cryptops* species.

Repair after damage

Species that increase the number of antennomeres during post-larval development are able to increase antennomere number after loss, but this may lead to atypically high numbers. Similarly, regeneration of lost end legs frequently leads to irregular spine arrangements and an atypically high number of prefemoral spines in scolopendrids (Fig. 1). This means that end leg characters of young individuals are more reliable than those of older ones. Verhoeff (1931), however, noted that regenerated end legs in *Cryptops* have a reduced number of tibial and tarsal teeth.

Regeneration of trunk legs may lead to atypical presence or absence of a tarsal spine, and these spines, especially on legs 19 and 20, are sometimes considered to be of taxonomic significance. There is, however, no direct evidence of this.

Wear

The forcipular coxosternal toothplates offer good taxonomic characters, but the teeth are subject to wear so that their basic pattern may be obscured (Figs 4, 5).

The end leg prefemoral spines and coxopleural spines of some scolopendrids can be lost, leaving only a very slight hump to indicate their point of attachment, which can be easily overlooked. Tarsal spines may also be lost and it is not always easy to detect this.

Accessory claws or claw spines may be subject to wear, so the size of these structures, which has been used as a taxonomic character in *Cryptops* by Lewis (2002), should be treated with caution.

Variable spine position

The number and disposition of spines on the coxopleural processes of the last leg-bearing segment are often of importance in scolopendrids, but their positions can vary. Spine migration appears to occur sometimes, so that for example an end spine may become a lateral spine (Fig. 1) (see Lewis 2002), and one spine may be replaced by two or more smaller ones. More observations are required on this phenomenon.

Longitudinal keels on tergites

Attems (1930) used tergites with sharp, finely serrate longitudinal keels, as opposed to only low rounded keels, or none, to separate species groups in *Otostigmus*. The keels are not, however, serrate in all specimens (Fig. 6). The character (sharp, serrate keels or not) is also used to separate two species of *Alipes,* despite the fact that Cook (1897) pointed out that the distinctness of the 'various longitudinal and oblique carinae' in specimens from Cameroon were 'subject to too much variation to be of systematic utility'. My impression is that in *Otostigmus* this character changes with age and varies geographically; it needs thorough investigation. Dobroruka (1968) used the character to separate two species in the doubtful genus *Congobius*.

Problematical characters

Five species of *Otostigmus* are characterised by tubercles on some posterior sternites (Fig. 7). Kraepelin (1903) suggested that they might be a malformation or a sexual character. The condition is unusual but widespread (NW Kashmir to Australia), and it may be pathological.

Size

In Nigeria, specimens of *S. morsitans* from Lake Chad were much larger than those from Zaria (Lewis 1978), and specimens collected on Rodrigues in the Indian Ocean were smaller than those from two offshore islets (Lewis 2002). The former situation may indicate different life history patterns influenced by climatic differences; the latter may be due to the absence of the large-bodied species *Scolopendra subspinipes* Leach, 1815 from the offshore islets.

Colour

Many scolopendrids are brightly coloured, showing yellow, orange, red, green, violet and black pigmentation. Unfortunately these colours fade on preservation, so that most museum specimens are a shade of brown, though sometimes with darker markings.

Whilst colour is a useful character in the field (the four northern Nigerian scolopendrids are clearly distinguishable by colour), it may be subject to considerable geographical variation. Detailed descriptions have been given for *S. morsitans* in Nigeria (Lewis 1978) and for *Scolopendra laeta* Haase, 1887 in Australia (Koch 1982). In the latter case five colour forms were recognised. Koch concluded that the change from one form to another is not dependent on a large genetic change, which is borne out by the fact that there is little variation in other morphological features; for this reason he treated them as 'informal groups which are geographically based.' By contrast the population of *S. morsitans* on Île aux Cocos off Rodrigues in the Indian Ocean, shows a remarkable degree of individual colour variation in a very small area (Lewis & Daszak 1996).

Attems (1930) separated two groups of *Cryptops* species on the basis that the trunk was either uniform yellow to olive brown, or in addition showed a rich green or black pigment. This presumably referred to the darkly pigmented connective tissue visible through the cuticle. Although many species lack dark pigmentation, its presence or absence probably does not indicate close relationship between species. Pocock (1891) based his description of *Cryptops doriae* Pocock, 1891 on three specimens, one of which had the tergites 'conspicuously marbled with black.' Lewis (2002) noted that *Cryptops daszaki* Lewis, 2002 from Mauritius lacked dark pigment, which was present in *C. niloticus* Lewis, 1967, but variable in *Cryptops decoratus* Lawrence, 1960. Whether the dark pigmentation is an adequate character to separate species in the absence of other distinguishing characters seems very doubtful.

The causes of colour variation in centipedes are elusive. Local and geographical colour morphs may be due to neutral alleles, or geographical variation may be due to climatic factors. The dark subcuticular pigmentation in some *Cryptops*, which is also seen in some geophilomorphs, could be due to a physiological factor.

THE UNKNOWN FUNCTION OF MANY TAXONOMIC CHARACTERS

The frustrating fact about centipede taxonomy is our lack of knowledge of the function of the structures utilised in discriminating taxa. Lewis (1985) suggested that the spines on the end legs of scolopendrids were species recognition characters, but other differences between species are not easily explained. An example in the Scolopendridae is the arrangement of teeth on the forcipular coxosternal toothplates, which cut into the prey like a spade or a tin-opener (Manton 1964). When in good condition these are important taxonomically, but the differences between species have not been explained. Similarly the tergite and sternite paramedian sutures, Manton's (1965) 'hinge lines', which she postulated permit easy shape changes of the segments, show consistent differences in some species of, for example, *Cormocephalus* (Figs 8, 9), yet cannot be explained in terms of function. The same is true of the various sutures on the head capsule and tergite 1 of some *Cryptops* species, and *Newportia* which, however, sometimes exhibit individual variation (Zapparoli 1989; Schileyko & Minelli 1998). It is difficult to escape the conclusion that many of these characters, like colour, may result from non-adaptive radiation controlled by neutral alleles. Alternatively some may be further species recognition characters.

DISCUSSION

Adis & Harvey (2000) estimate that there are 515–616 described species of Scolopendromorpha, and that the total number of species is between 700 and 800. The number of valid described species is almost certainly too high. I estimate that the number of *Cryptops* species will at least be halved as type material is re-evaluated. A checklist of Indian Scolopendromorpha (Khanna 2001) records 101 species, but this may be far from the true figure. For example, it lists six species of *Digitipes* all described by Jangi & Dass (1984). This genus is otherwise known only from two species from the Democratic Republic of the Congo. The close resemblance to some *Otostigmus* species suggests that the material should be re-examined.

With limited numbers of specimens from widely scattered localities and considerable variation, it can be difficult to decide whether one is dealing with one or several scolopendromorph species, for example *Otostigmus aculeatus* Haase, 1887 in China, and Vietnam (Lewis 2001). The state of knowledge is such that even for common species, the characteristics of each specimen need to be recorded, which is time-consuming but necessary. Accurate illustration is essential as good figures can better convey data than a written description, and avoid misconceptions stemming from the latter. Their value cannot be stressed too much. The nature of the setae and cuticular surfaces, particularly in some scolopendrid genera where the latter may be characterised as rugose, spined, spine-streaked, striate, tuberculate etc., need to be examined by scanning electron microscopy. Much more data are required on spiracle and antennal structures, but the information may be more useful in distinguishing genera than species. Again the investigations would require scanning electron microscopy. Furthermore as sex is difficult to determine or not recorded in scolopendromorphs, there may be a number of unrecognised parthenogenetic species.

As Crabill (1960) pointed out, a number of terms need to be defined and a consensus needs to be reached on a standardised terminology.

In some cases all that we can presently attempt is to identify groups of closely related populations, the status of many, but perhaps not all, to be resolved at a later stage when more data are available. The situation was well described by Kondrashov (1992), who expressed the view that 'there are 'good' species … essentially homogeneous and drastically different from relatives' but 'to argue about whether similar but separated populations are already different species is as futile as to discuss how many grains constitute a heap… Even sympatric forms are frequently isolated incompletely… In such cases we cannot discover species like new islands but, instead face continuous diversity and have to describe it.' It must be accepted that progress will be slow and it is inevitable that errors will continue to be made, as mistakes only become obvious after the accumulation of further data.

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